

THE TRIBE BROSCINI IN MEXICO:
RAWLINSIUS PAPILLATUS, NEW GENUS AND NEW SPECIES
(INSECTA: COLEOPTERA: CARABIDAE),
WITH NOTES ON NATURAL HISTORY AND EVOLUTION

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ABSTRACT

Based on structural and ecological features of adults and larvae, particularly absence of standard fixed dorsal setae in adults, and the habitat of torrential mountain streams, *Rawlinsius papillatus* (type locality: Mexico, Guerrero, Sierra Madre del Sur, 26 km NW El Paraiso, 1800 m) is described as a new monobasic genus and species. This species is placed in the tribe Broscini, subtribe Broscina (Northern Hemisphere assemblage, excluding *Axonya* Andrewes and *Broscodes* Bolivar) on the basis of common possession of the unique set of features used to characterize these higher taxa. A key distinguishes *Rawlinsius* from the other New World genera of Broscini. Separated widely both morphologically and geographically from other New World Northern Hemisphere Broscina, *R. papillatus* is postulated to be a relictual taxon, its present isolation indicating past connections to a more broadly distributed northern broscine lineage.

KEY WORDS: systematics, evolution, biogeography, relicts, Mexico, Coleoptera, Carabidae

INTRODUCTION

Toward evening on 3 July 1982, it got dark. It got dark before lepidopterist John Rawlins had reached his destination higher up in the Sierra Madre del Sur, so he did what he always does in such circumstances. He stopped at the first convenient place, unpropitious as it was, and set up his sheet and traps for a night of serendipitous collecting. It is to this behavior that we owe one of the most extraordinary carabid discoveries of the century.

Always a good general collector, Rawlins wandered from the sheet from time to time to search for other insects. He found an extraordinary tenebrionidlike beetle (Fig. 1, 2, 3A) wading in the water along the shallow edge of a rapid stream just where the stream dropped over a 3-m vertical face. He collected the single female specimen, pinned it, and put it in a box, but its peculiar appearance and behavior remained in his mind.

In the autumn of 1985, Rawlins showed a box of Mexican beetles to Davidson, including the mysterious wading beetle. Much excitement ensued when they realized the beetle belonged in the Carabidae and was of uncertain tribal affinities. Tribes were eliminated one by one until it was decided (based largely on Gestalt) that the beetle belonged in the Broscini or perhaps in a new tribe somewhere in the vicinity of Broscini. But the nearest broscines were several thousand kilometers to the north and south, and, with only a single female, it was impossible to be

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Fig. 1.—Dorsal habitus of *Rawlinsius papillatus*, n. gen., n. sp. Male, total length, ca. 17 mm.

certain. The importance of the discovery seemed to merit an effort to obtain further material, so Rawlins and Davidson returned to the site where the specimen had been found.

They arrived at the site on 8 August 1986 and waited until dark. They approached the wet cliff face (Fig. 3C) and, still a couple of meters away, were excited to see the gun-metal blue glint of several adult beetles (Fig. 3A, B) in the light of the headlamps. Within half an hour, they spotted ten adults and one larva, collecting most of them while leaving a few undisturbed to observe their behavior



Fig. 2.—Ventral habitus of *Rawlinsius papillatus*, n. gen., n. sp. Male, total length, ca. 17 mm.

before collecting them as well. The following night, two more adults and another larva were collected, and no further specimens could be found. Other streams along the road were searched without success. During the ensuing two weeks, several other streams in Guerrero and Oaxaca were searched, also without success.

With 13 adults and two larvae, sufficient material was available for study and dissection. Because of his experience with Broscini and with Mexican Carabidae generally, G. E. Ball was invited to participate in the study of this remarkable species. Examination of the male genitalia (including internal sac) revealed features



Fig. 3.—Photographs of living *Rawlinsius papillatus*, n. gen., n. sp., and of the type locality. A, B, *Rawlinsius papillatus*: A, dorsal aspect; B, dorsal aspect, head and prothorax. C, vertical water-covered rock face, microhabitat of *R. papillatus*, n. gen., n. sp.

indicating an affinity to the tribe Broscini, and other features pointed in that direction. But this seemed unlikely because broscines were not known to occur within several thousand kilometers of southern Mexico. Nonetheless, the authors began with the assumption that the specimens represented an undescribed species that could not be placed in any known genus, but that belonged probably in the Broscini.

To make this species and genus known, we offer the following descriptions and illustrations. We develop a context for understanding these taxa in terms of clas-

sification of the Carabidae (in particular, the Broscini), and in terms of evolutionary, principally biogeographical, considerations.

MATERIALS, METHODS, AND TERMS

Materials

This study is based on examination of 13 adults and two larvae representing a new genus and species. Additionally, material housed in the collections of the Carnegie Museum of Natural History and in the E. H. Strickland Museum, University of Alberta, representing all of the known New World genera of Broscini, was examined.

The two larvae that most probably belong to the new species are discussed briefly in terms of the tribal placement of this species and comparative behavior of larvae and adults. A formal description of the larvae is excluded from this study and will be done separately.

Methods

Techniques

Dissections and illustrations were made using standard techniques, as described, for example, by Shpeley and Ball (1993:10–11).

The only measurements reported are: overall length, the sum of length of head from tip of mandibles to postocular transverse depression + length of pronotum + length of elytra (from basal ridge, along suture) to apex; width is transverse distance across the elytra at their widest point.

Species Recognition and Ranking

In terms of known New World broscines, this taxon was recognized as a new species because of its distinctive combination of structural features. Similarly, the large degree of difference from all other known broscine genera was used to place the species in a genus of its own.

Relationships

These were inferred on the basis of postulated shared derived (synapomorphic) character states (Hennig, 1966:90–91; Ax, 1987:4).

Terms for Structural Features

Most of the words used by us to designate details of structures are recorded in textbooks of general entomology and are used by coleopterists generally. Other words, required to designate particular structural features or parts thereof, are not in general use. We provide information about these words here.

Microsculpture

A “sculpticell” (Fig. 4B:sc) is the space enclosed on the surface of the cuticle by adjacent microlines of the integumental system of microsculpture (Allen and Ball, 1980:485–486).

Body Parts

The term “segment” is restricted to those body parts that reflect embryonic somites; thus, somitelike portions of the abdomen are referred to as segments. Abdominal segments and their appendages are designated by Roman numerals

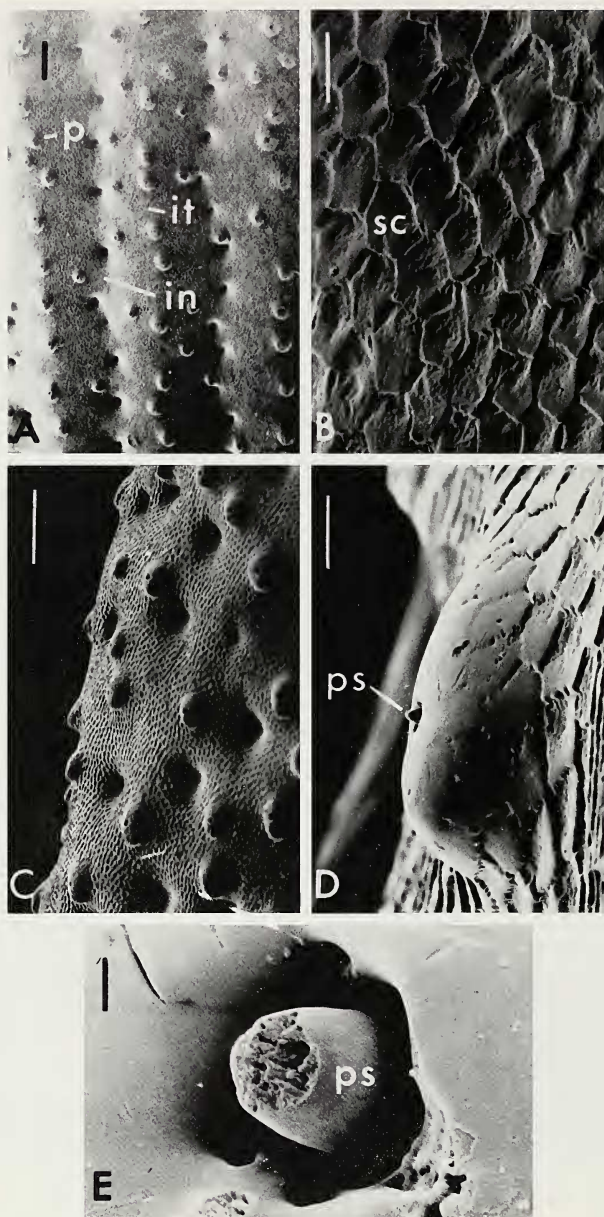


Fig. 4.—SEM photographs of macrosculpture and microsculpture of basal portion of left elytron of *Rawlinsius papillatus*, n. gen., n. sp. A, C, macrosculpture, dorsal aspect, lower and higher magnification, respectively. B, microsculpture, dorsal aspect, mesh pattern. D, papilla, lateral aspect. E, papillar seta, dorsal aspect. Abbreviations: in, stria; it, interval; p, papilla; ps, papillar seta; and sc, sculpticell. Scale bars: A, C = 100 μ m; B, D = 10 μ m; and E = 1 μ m.

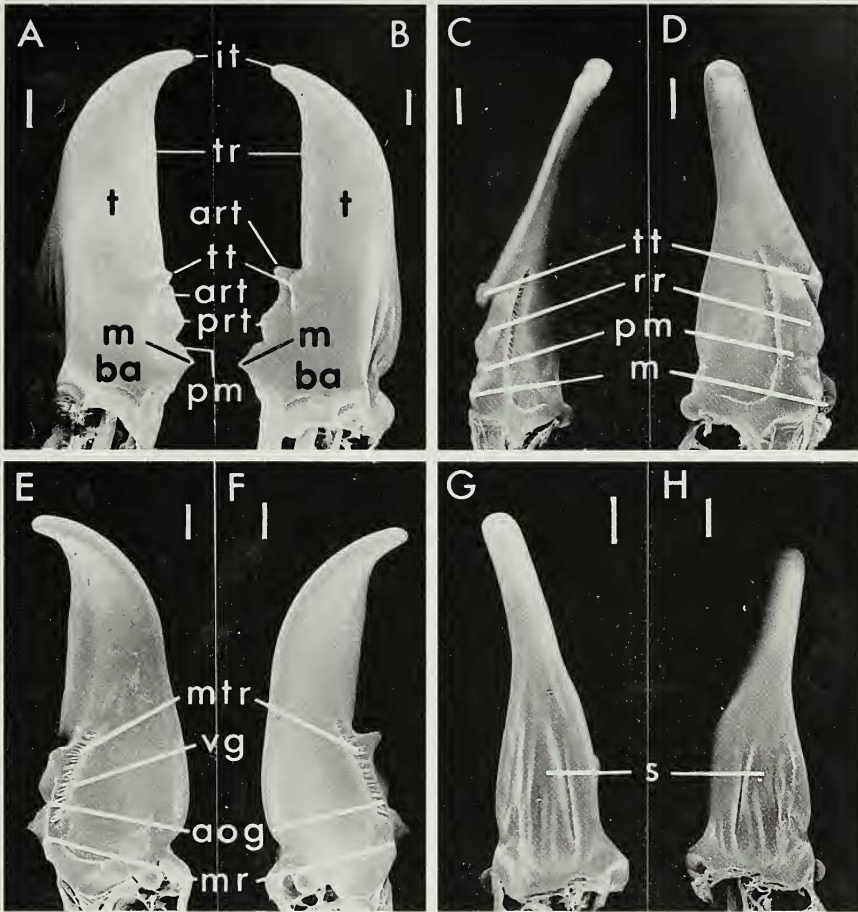


Fig. 5.—SEM photographs of mandibles of *Rawlinsius papillatus*, n. gen., n. sp. A, C, E, G, left mandible, dorsal, occlusal, ventral, and lateral aspects, respectively. B, D, F, H, right mandible, dorsal, occlusal, ventral, and lateral aspects, respectively. Abbreviations: aog, anterior occlusal groove; art, anterior retinacular tooth; ba, basal area; it, incisor tooth; m, molar tooth; mr, ventral molar ridge; mtr, microtrichia of ventral groove; pm, premolar tooth; prt, posterior retinacular tooth; rr, retinacular ridge; s, scrobe; t, terebra; tr, terebral ridge; tt, terebral tooth; and vg, ventral groove. Scale bars = 200 μ m.

corresponding to the respective somites. The first complete sternum is III, and the last one (pregenital) normally exposed is VII. For numbering the somites associated with the genitalia, we follow Bills (1976).

Portions of appendages are designated by the suffix “-mere,” the prefix depending upon the appendages in question, e.g., antenno-, palpo-, tarso-, etc.

Mandibles

Acorn and Ball (1991) proposed a general system for recognizing and naming elements of the mandibles. The names provided below (Fig. 5) reflect this general system, as applied to the mandibles of *Rawlinsius*.

Labium

The word “ligula” is used for glossae + paraglossae. In turn, the fused, scler-

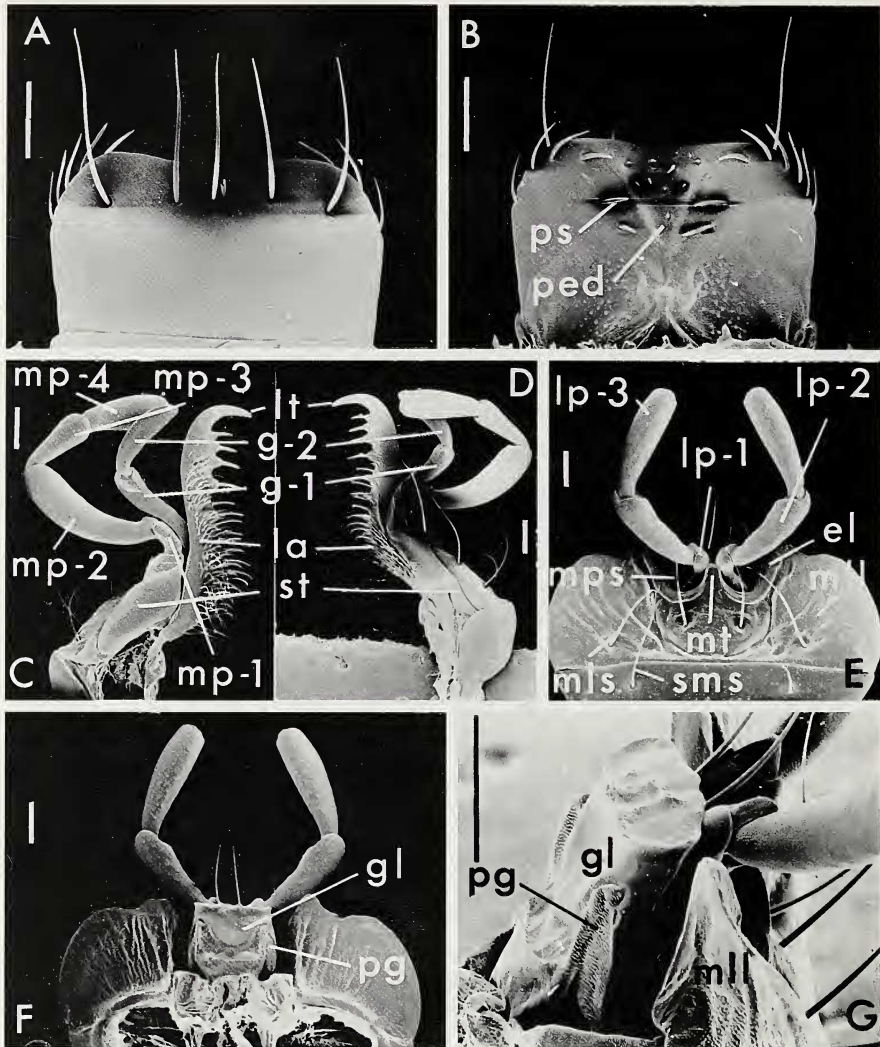


Fig. 6.—SEM photographs of labrum, maxilla, and labium of *Rawlinsius papillatus*, n. gen., n. sp. A, B, labrum, dorsal and ventral aspects, respectively. C, D, left maxilla, dorsal and ventral aspects, respectively. E, F, G, labium: E, F, ventral and dorsal aspects, respectively; G, right lateral aspect of prementum and lateral lobe of mentum. Abbreviations: el, epilobe (mentum); g-1, g-2, galeomeres 1 and 2, respectively; gl, glossal sclerite; la, lacinia; lp-1 to lp-3, labial palpomeres 1–3, respectively; lt, lacinial tooth; mll, mentum, lateral lobe; mp-1–mp-4, maxillary palpomeres 1–4, respectively; mls, mental lateral seta; mps, mental paramedial seta; mt, mental tooth; ped, pedium; pg, paraglossa; ps, parapodial seta; sms, submental seta; and st, stipes. Scale bars = 200 μ m.

otized glossae (Fig. 6F:gl), characteristic of beetles generally, are termed collectively the “glossal sclerite” (Ball and Shpeley, 1983:746).

Elytra

The dorsal surface of the elytra (Fig. 7A) is divided into intervals and striae. Stria is understood to be a collective rather than a descriptive noun, and it encompasses the structures in several character states, not necessarily a grooved or

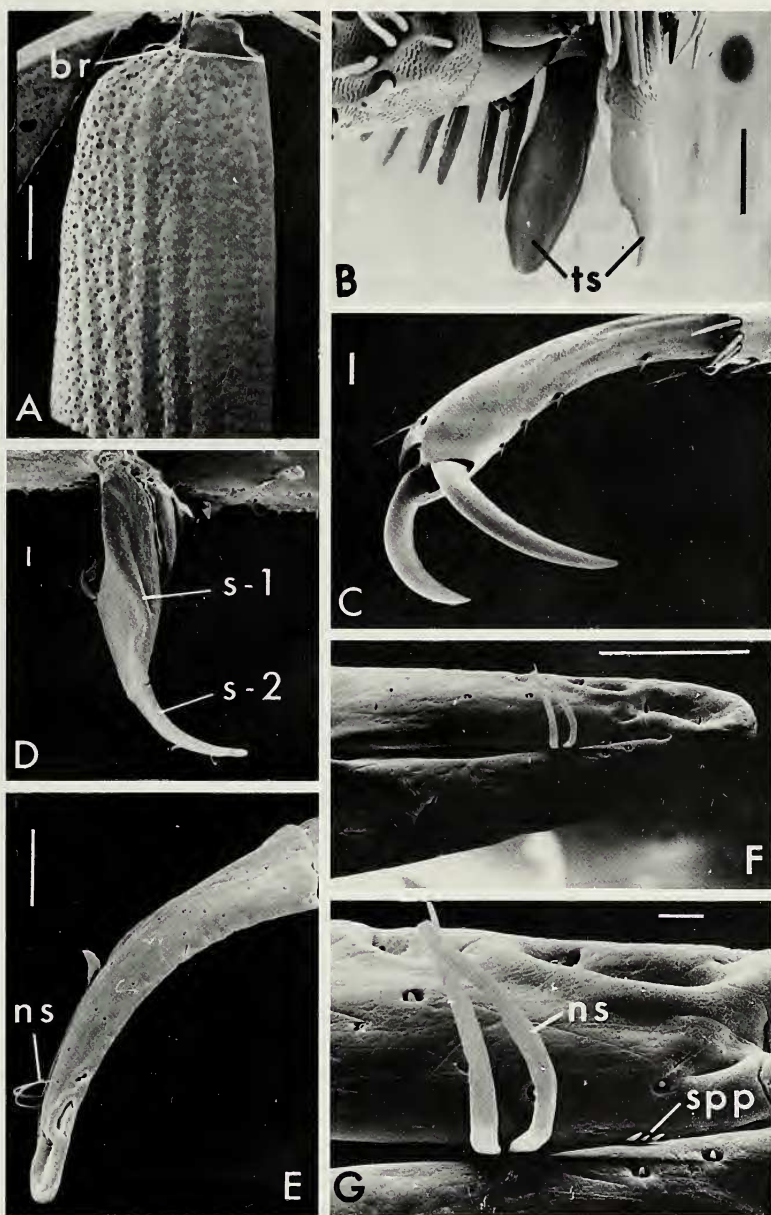


Fig. 7.—SEM photographs of elytra, legs, and ovipositor of *Rawlinsius papillatus*, n. gen., n. sp. A, left elytron, basal portion, dorsal aspect. B, tibial spurs, left hind leg, medial aspect. C, left hind tarsomere 5 and claws, medial aspect. D–G, ovipositor: D, left stylomeres 1 and 2, lateral aspect; E, left stylomeres 2, lateral aspect; F, G, stylomeres 1 and 2, ventral aspect. Abbreviations: br, basal ridge; ns, nematiform seta; s-1 and s-2, stylomeres 1 and 2, respectively; spp, sensory pit peg; ts, tibial spurs. Scale bars: A = 1 mm.; B–F = 100 μ m; G = 10 μ m.

striate character state. A stria can be a complete or abbreviated groove, a series of disconnected grooves or dashes, a row of punctures, or completely absent. The neologism *interneur* (Erwin, 1974:3–5), coined to replace stria, is abandoned due to Cooper's (1990) cogent arguments.

Male Genitalia

The internal sac of members of the subtribe *Broscina* is characterized by a very complex armature (Fig. 10A, B, F–H). To facilitate reference to details, Ball (1956) designated two of the sclerites as x and y, respectively. There is also an apical plate (a), with an extensive and complex field of microtrichia.

Ovipositor

Terms for sclerites of the female genital segments (VIII–X in Coleoptera) and their appendages (Fig. 7D–G, 11A) have a complex history, occasioned principally by different views among authors about homology of the sclerites. Ball and Shpeley (1983:746) explain terms used for sclerites and setae, and orientation of this complex of sclerites. Note that for the stylomeres, the surfaces that are ventral in the infolded position are lateral when the ovipositor is extended; thus, such surfaces are designated as lateral, and the other surfaces are designated accordingly.

We make reference here only to the appendages putatively of segment IX (or IX + X; Bils, 1976), comprising two stylomeres (s-1 and s-2; Fig. 7D, 11A). Noonan (1973:275) explains the morphological basis for regarding the stylus as bipartite, rather than as "coxite" and "stylus" (Tanner, 1927). Stylomere 2 is referred to by Deuve (1993) as gonopod IX. Also, he refers to the sensory furrow, or pit (Fig. 7F, G) as the subapical setose organ, in which is inserted a pair of relatively long nematiform setae and a varied number of short sensory pit pegs (Fig. 7F, G:ns, spp).

TAXONOMIC TREATMENT

Tribe Broscini, Characters and Relationships

To determine placement of *Rawlinsius papillatus*, the genus and species described below, it is necessary to consider some general matters about broscine carabids. According to Erwin (1985:467–468) and other authors, the postulated relationships of the Broscini are indicated by the following classification.

- Division Melaeniformes
- Subfamily Broscinae
 - Supertribe Melaenitae
 - Tribe Melaenini
 - Tribe Cymbionotini
 - Supertribe Broscitae
 - Tribe Broscini
 - Supertribe Apotomitae
 - Tribe Apotomini

The sister group of the Melaeniformes is the Psydriformes. The derived feature for this complex (i.e., Melaeniformes + Psydriformes = Harpalinae of Horn [1881] and others) is the conjunct middle coxae. The only derived feature for the

Melaeniformes seems to be the pedunculate body, a feature that Lindroth (1961b: 169) suggested might be a synapomorphy for Broscini + Scaritini.

Within the Melaeniformes, most of the supposedly diagnostic features of the tribes prove not to be. Even the elaborate sclerotization of the internal sac of the subtribe Broscina is shared with at least the melaenines and cymbionotines, but not with the Apotomini, males of which lack complex armature. As well, this complex armature occurs in males of the seemingly unrelated paussoid complex and the Elaphrini. Goulet (1983:460), however, concluded that, based on structural details of the male genitalia, the tribe Elaphrini probably was related to the subtribe Broscina and to the tribe Melaenini.

Evidence for including *Rawlinsius papillatus* in the tribe Broscini is based on the following combination of diagnostic features: integument glabrous, without vestiture of short setae; prothoracic–mesothoracic junction pedunculate, with scutellum short and broad and located anteriorly to the elytral humeri; head with occiput with a transverse groove; mouthparts as described below, especially the bisetose labial palpomere 2 and the toothed mentum; middle coxal cavities conjunct; fore tibia anisochaetous; elytron without discal setae, and with lateral margin posteriorly uninterrupted by a plica; parameres of male genitalia long and setose apically; and ovipositor stylomere 2 without marginal ensiform setae. The armature of the internal sac of the male genitalia (sclerite x with pair of apical flanges—f, Fig. 10B, F, G) is typical of the Northern Hemisphere assemblage of the subtribe Broscina.

With the exception of the flanges on sclerite x of the internal sac, the features recorded above are plesiomorphic within the division Melaeniformes and subfamily Broscinae. Together, however, they define the tribe Broscini (in a formal, if not phylogenetic, sense). More particularly, they define the Northern Hemisphere assemblage of the subtribe Broscina (excluding *Axonya* and *Broscodes*), and their possession prevents inclusion of *Rawlinsius* in any other suprageneric melaeniform taxon.

The following ten genera of Broscina are represented in the New World, grouped (Ball, 1956; Roig Juárez, 1995; Roig Juárez and Ball, 1995) as follows:

Subtribe Baripodina: *Baripus* Dejean 1828 (Argentina, Chile, Uruguay; 22 species);

Subtribe Creobiina: *Cascellius* Curtis 1839 (Argentina, Chile; two species); *Creobius* Guérin-Ménéville 1838 (Argentina, Chile; one species); and *Nothocascellius* Roig Juárez 1995 (Argentina, Chile; two species);

Subtribe Broscina: *Broscodera* Lindroth 1961a (Nearctic; one species); *Broscus* Panzer 1813 (many Palearctic species, one species introduced in the Nearctic); *Miscodera* Eschscholtz 1830 (Holarctic; one species); *Nothobroscus* Roig Juárez and Ball 1995 (Chile; one species); *Rawlinsius*, n. gen. (Mexico; one species); and *Zacotus* LeConte 1869 (Nearctic; one species).

The following key, based on external features of adults, allows identification of the broscine subtribes and genera of the New World.

Key to Subtribes and Genera of Broscini in the New World

(Based in part on Roig Juárez and Ball, 1995:303, and Roig Juárez, 1995:53)

- 1 Eyes emarginate anteriorly; prosternum with pair or cluster of setae at apex of intercoxal process; elytron basally without parascutellar seta; abdominal sterna V–VII each with

complete transverse groove. Argentina, Chile, Uruguay. (Subtribe Baripodina) *Baripus* Dejean

1' Eyes not emarginate, anterior margin evenly rounded in outline; prosternum with apex of intercoxal process asetose; elytron without or with parascutellar seta; abdominal sterna V-VII each with or without transverse groove, smooth or with one or two lateral grooves, each side 2

2 (1') Labium with glossal sclerite apically quadrisetose. (Subtribe Creobiina) 3

2' Labium with glossal sclerite apically bisetose (Fig. 6E-G). (Subtribe Broscina) 5

3 (2) Head with three or more pairs of supraorbital setae; pronotum with more than two pairs (four pairs in most individuals) of lateral marginal setae; abdominal sterna V-VII anteriorly without transverse groove. Argentina, Chile *Creobius* Guérin-Ménéville

3' Head with one pair of supraorbital setae; pronotum with two pairs of lateral marginal setae; abdominal sterna V-VII anteriorly with transverse groove 4

4 (3') Eyes convex; elytra (in profile) with apex on same plane as epipleura; male with mid tarsomeres 1-3 and fore tarsomeres 1-4 with adhesive vestiture. Argentina, Chile *Cascellius* Curtis

4' Eyes flatter; elytra (in profile) with apex downcurved below plane of epipleura; male with fore tarsomeres 1-2 or 1-3 with adhesive vestiture, mid tarsomeres without vestiture. Argentina, Chile *Nothocascellius* Roig Juárez

5 (2') Dorsal surface without fixed setae (mandibular scrobal, clypeal, supraorbital, lateral pronotal, elytral-parascutellar, discal, or lateral umbilical); metepisternum longer than wide; elytra with dorsal surfaces papillate; abdominal sterna V-VII with transverse groove close to anterior margin; macropterous. Mexico *Rawlinsius*, new genus

5' Dorsal surface with fixed setae (at least clypeal, supraorbital, lateral pronotal, and elytral lateral umbilical); metepisternum longer than wide, or as long as wide at base; elytra with dorsal surfaces smooth, not papillate; abdominal sterna V-VII without transverse groove; macropterous or brachypterous 6

6 (5') Labial mentum with tooth bifid at apex and with paramedian pits; elytron without parascutellar seta; dorsal integument black. Chile *Nothobrosca* Roig Juárez and Ball

6' Labial mentum (Fig. 6E) with tooth simple at apex, with or without paramedian pits; elytron with parascutellar seta; dorsal integument black or coppery and green. Nearctic or Holarctic 7

7 (6') Pronotum with single pair of marginal setae (posterior pair lacking); pronotum markedly constricted posteriorly, with deep transverse groove; mentum with paramedian pits. Northern Holarctic *Miscodera* Eschscholtz

7' Pronotum with two pairs of marginal setae; pronotum not markedly constricted posteriorly, without deep posterior groove; mentum with or without paramedian pits 8

8 (7') Head with frons and vertex more or less grooved and rugose; mentum without paramedian pits. Nearctic, Pacific Northwest *Zacotus* LeConte

8' Head with dorsal surface smooth, except frontal impressions and sparse punctation; mentum with or without paramedian pits 9

9 (8') Middle femur with row of about six setae ventrad on anterior surface; tarsomeres 1-4 with dorsal surfaces smooth, glabrous; eight or nine setae in elytral umbilical series; mentum without paramedian pits; overall length of body about 20 mm. Palaearctic; introduced in North America, known only from coastal localities in maritime Canada . . . *Brosca* Panzer

9' Middle femur with row of not more than three setae ventrad on anterior face; tarsomeres 1-4 with dorsal surfaces rugulose and sparsely setose; mentum with paramedian pits; three

or four setae in elytral umbilical series; overall length of body about 10 mm. Western North America *Broscodera* Lindroth

Rawlinsius, new genus

Type Species

Rawlinsius papillatus, new species; here designated.

Generic Name

Eponym, masculine, based on the surname of the collector of the first specimen, John E. Rawlins, Carnegie Museum of Natural History. We take great pleasure in naming this new genus after our friend and colleague. His extraordinary perseverance in the field and great breadth of coverage when collecting have led to this and many other fine discoveries.

Recognition of Adults

See key.

Description

None required because the genus is monobasic, and its characters are the same as those of its type species, which is described below.

Larvae

We note here the features that establish the two larvae as members of the tribe Broscini, based on the diagnostic features indicated by Jeannel (1941:288), van Emden (1942:17), and Thompson (1979: 225, 247): head with cervical grooves; antenna with antennomere 1 longest of antennomeres 1–4; outer lobe of maxilla with article 1 longer than 2, inner lobe represented by a stout seta; urogomphus longer than the pygopodium; and each tarsus terminated in a single claw. In Moore's (1964:244) key to the four genera of Broscini with known larvae, the putative *Rawlinsius* larvae exhibit the diagnostic features of *Broscus*, type genus of the subtribe Broscina. Two distinctive features of the *Rawlinsius* larvae are the mandibles with two teeth (a feature shared with Omophronini), and the moderately densely setose integument.

Geographical Distribution

See Figure 12 and under species description below.

Chorological Affinities

The only known locality of this genus is isolated by about 3000 km from the range of other Northern Hemisphere broscines, and by about 7500 km from the range of south temperate New World broscines.

Phylogenetic Relationships

The flanges on sclerite x of the male internal sac (Fig. 10B, F, G:f) represent a putative synapomorphy for a group of Palaearctic and Nearctic members of the subtribe Broscina. Because males of *Rawlinsius* have these flanges, we postulate that the genus is a member of this northern assemblage of the subtribe Broscina. Within this assemblage (Northern Hemisphere Broscina, excluding *Axonya* Andrewes and *Broscodes* Bolivar), *Rawlinsius* is distinctive in the following features of the male genitalia: basal bulb open widely, opening extended onto dorsal surface; and sclerite x of the internal sac neither markedly constricted basally nor terminated in a short subuliform projection (Roig Juñent, personal communication). If these genitalic features of *Rawlinsius* prove plesiomorphic, this genus may be the adelphotaxon to the other northern broscine genera, with exclusions as noted above.

Rawlinsius papillatus, new species

Type Material

Holotype male, labelled: "MEXICO: Guerrero/ 26 km NW El Paraiso/ 1800 m.

8 Aug 1986/ R. Davidson, J. Rawlins". Paratypes 12, with five males and six females labelled as holotype. One female labelled same as holotype, except: "July 3, 1982, J. Rawlins". Holotype and ten paratypes at Carnegie Museum of Natural History; one male paratype deposited at University of Alberta, Strickland Museum; one female paratype deposited at Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México.

Type Locality

The locality indicated above for the type series, more specifically, is at 17°29'N, 100°12'W in the Sierra de Atoyac de Alvarez section of the Sierra Madre del Sur, Guerrero, Mexico. This is according to the Carta de México Topográfica 1: 250,000 (Anonymous, 1982). The road had been washed out and rebuilt in places in a different direction, and several maps examined each showed the trend of the road in a different orientation from El Paraiso (NW, N, NNE). Without a Global Positioning System device, it was impossible to be certain of the exact latitude and longitude or general direction. Nonetheless, there is only one road from Atoyac through El Paraiso, continuing over the summit just below Cerro Teotepec, and dropping down the east face to Filo de Caballo and Xochipala. The exact straight-line distance from El Paraiso to the type locality is not known. Traveling approximately 26 km from El Paraiso along the road to Cerro Teotepec will take the interested collector to the proper site. The detailed description of habitat in the present paper should allow one to recognize the microsite. Vargas-Fernandez et al. (1992:46–55) provide a good description of the region, an illustration (fig. 3, p. 51) of the drainage system, an interpretation of the position of the road, and an illustration (fig. 6, p. 55) of the vegetation profile.

Specific Epithet

A Latin masculine adjective, referring to the papillate dorsal surface of the elytra (Fig. 4A, C).

Recognition

Adults are rather large carabids (overall length 15–20 mm), with dark integument that is metallic blue-green when wet (Fig. 3A, B). The dorsal surface is devoid of setae, including the standard fixed setae: clypeal and supraorbital of the head; antennal scape, apex of pedicel, and antennomere 3; lateral pronotal; and parascutellar, discal, and lateral umbilical of the elytra. Lacking also are the scrobal setae of the mandibles, the presence of which is a ground-plan feature of the tribe Broscini.

Description

Habitus as in Figures 1, 2, 3A, B. Attitude partly hypognathous. Overall length of body, males, 15–18 mm (mean 16.9 mm); females, 18–20 mm (mean 19.1 mm). Maximum width (elytra), males, 5.5–6.0 mm (mean 5.7 mm); females, 6–7 mm (mean 6.4 mm). Surface glabrous.

Color and Luster.—Dorsal surface when dry predominantly black, tinged with metallic blue-green to purple (color especially evident on surface viewed obliquely); dorsal surface when wet predominantly bright metallic blue-green (Fig. 3A, B). Ventral surface, mouthparts (including palpi), and legs dark piceous to black. Setae of tibiae, tarsi, mentum, and labrum yellow-brown. Dorsal surface rather dull when dry; shiny when wet.

Microsculpture.—Dorsal surface granulate, with mesh pattern predominantly approximately isodiametric, sculpticells slightly elongate (Fig. 4B); sculpticells small, each with surface slightly convex. Ventral surface with mesh pattern more transverse, sculpticells with surface flat.

Macrosculpture.—Head with clypeus, frons, and vertex rather coarsely, moderately densely punctate, occiput more sparsely punctate or impunctate; frons and vertex laterally grooved and ridged vermiculately. Ventral surface with genae and postgenae moderately densely, coarsely punctate; gula smooth. Pronotum coarsely, densely punctate anteriorly, laterally, and posteriorly; disc centrally ru-

glose, with rather prominent transverse rugulae. Proepipleura shallowly to deeply punctate. Propodeum and prosternum punctate and vermiculately rugulose. Pterothoracic pleura, lateral areas of sterna, and lateral areas of hind coxae coarsely and sparsely punctate, central parts of sterna smooth. Elytral surface irregular, with numerous small papillate swellings (Fig. 4A, C–E) mainly in longitudinal rows centrally on intervals (Fig. 4A), but not confined to such position. Striae with coarse irregular punctures. Elytral epipleura with short row of dashlike punctures near humeri.

Head.—More or less quadrate in outline. Dorsally, clypeus somewhat swollen posteriorly; frontal impressions indistinctly delimited, basinlike; occiput grooved shallowly, transversely; postocular areas inflated. Laterally, paragenae broad anteriorly, tapered beneath eye to slightly narrower than width of antennal scape. Eyes moderate in size, slightly convex. Antennae filiform; antennomeres 1 (scape)—4 glabrous with apical fixed setae only on 4; antennomeres 5–10 with dense covering of short sensory setae and apical fixed setae present; scape rather thick; pedicel short; antennomere 3 elongate, about 1.25 length of antennomere 5; antennomeres 4–11 as in most *Broschini*.

Labrum.—Labrum (Fig. 6A, B) rectangular, transverse; dorsal surface (Fig. 6A) with six long setae, inserted preapically in five punctures, middle pair sharing same puncture. Ventral surface with epipharynx (Fig. 6B) very simple, reduced markedly, pedium (ped) short, narrowly triangular, with few peglike sensilla; parapedal setae (ps) few; crepis and parapedal projection not evident.

Mandibles.—Mandibles (Fig. 5A–H) trigonal in outline, slightly curved ventrally; scrobes grooved, without scrobal seta apically (Fig. 5G, H). Left mandible (Fig. 5A, C, E, G) in dorsal aspect (Fig. 5A) with short incisor tooth (it), rounded apically; terebra (t) long, occlusal surface with supraterebral ridge indistinct, terebral ridge (tr) nearly straight, curved slightly; retinaculum short, anterior and posterior retinacular teeth (art, prt) indistinct, blunt apically; and molar tooth (m) short; occlusal surface (Fig. 5C) with posterior occlusal groove absent; ventral surface (Fig. 5E) with molar ridge (mr) short and with ventral groove (vg) short, about one-third length of mandible; microtrichia (mtr) relatively sparse. Right mandible (Fig. 5B, D, F, H) similar to left, except: terebra narrower; terebral tooth smaller; retinaculum with anterior and posterior teeth more prominent, retinacular ridge (rr) concave; and molar tooth more prominent.

Maxillae.—Maxillae (Fig. 6C, D) with stipes (st) with three lateral setae. Lacinia (la) with apical tooth (lt) thick, markedly curved mediad in relation to long axis of lacinia; occlusal surface with four prominent, thick spines in apical half; basal half with row of relatively large, curved setae; dorsal surface with sparse vestiture of smaller setae. Galeomeres 1 and 2 (g-1, g-2) subequal in length. Palpomeres 3 and 4 (mp-3, mp-4) subequal in length, each about one-half length of palpomere 2 (mp-2); palpomere 1 (mp-1) about one-third length of palpomere 2.

Labium.—Labium (Fig. 6E–G), ventral aspect (Fig. 6E). Submentum with single pair of setae (sms); mentum with two pairs of setae, one pair paramedial (mps), and one pair more lateral (mls). Mentum transverse, anteriorly with broad sinus and prominent medial tooth (mt); lateral lobes (mll) broad, each broadly rounded laterally, apical margin sinuate; epilobes (el) clearly marked throughout length. Ligula with glossal sclerite (gl) bisetose apically, rather broad and thick (Fig. 6F, G), apical margin subtruncate; paraglossae not visible; dorsal surface (Fig. 6F) with paraglossae (pg) evident, each with vestiture of numerous short microtrichia. Palpomere 2 (lp-2) bisetose; palpomeres 2 and 3 (lp-2, lp-3) subequal in length; palpomere 1 (lp-1) about one-fifth length of palpomere 2.

Prothorax.—Pronotum rather narrow, with length and width subequal, but wider than head across eyes, and base distinctly wider than apex; anterior (apical) margin slightly concave; posterior margin slightly lobed medially; lateral margins rounded anteriorly, sinuate posteriorly, epipleuron visible in situation from dorsal aspect; anteriolateral angles rounded narrowly, not projected forward; posteriolateral angles about rectangular, but narrowly rounded; anterior and posterior margins not beaded; anterior and posterior transverse impressions barely indicated, median longitudinal impression distinct in middle part of pronotum; anterior surface generally convex, slightly flattened dorsally, without lateral grooves and surface rounded evenly each side to epipleural margin. Prosternum with intercoxal process not margined apically.

Pterothorax.—Metepisternum very long and narrow; metepimeron narrow, truncate posteriorly.

Scutellum.—Short, broad, rounded posteriorly; mostly concealed beneath posterior margin of pronotum.

Elytra.—Long and slender, depressed anteriorly basal ridge (Fig. 7A:br). Basal ridge thick laterally, to level of interval 6, extended to suture as thin line not elevated above surface posteriorly; apical margin complete, not interrupted laterally by plica; apical declivity sloped ventrally slightly and gradually. Striae (Fig. 4A:in) broad, shallow, indistinctly delimited; parascutellar stria evident. Intervals (Fig. 4A:it) slightly convex.

Wings.—Fully developed (Fig. 8); venation as in most Carabidae; oblongum cell (o) large; wedge cell (w) small.

Legs.—Long and slender (Fig. 9A): hind leg, length trochanter/length femur 0.19; dorsal surface of

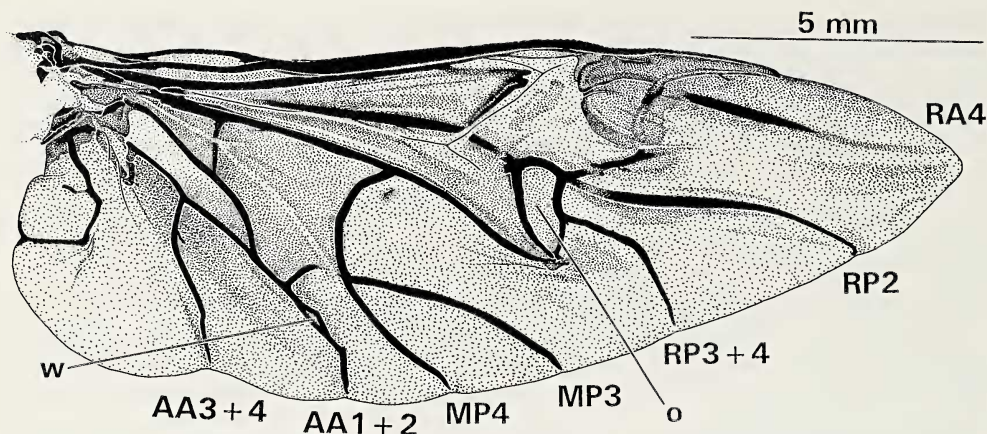


Fig. 8.—Right hind wing of *Rawlinsius papillatus*, n. gen., n. sp., dorsal aspect. Abbreviations: AA 1 + 2, anterior anal vein 1 + 2; AA 3 + 4, anterior anal vein 3 + 4; MP 3, posterior medial vein 3; MP 4, posterior medial vein 4; o, oblongum cell; RA 4, anterior radial vein 4; RP 2, posterior radial vein 2; RP 3 + 4, posterior radial vein 3 + 4; w, wedge cell.

femora with small tubercles, these evanescent on other faces; middle femur with few setae proximally; anterior surface of front tibia, most of middle and hind tibiae, and dorsal surfaces of tarsomeres rugulose (Fig. 7C); proximal half of tibiae, especially middle and hind tibiae, with three indistinct carinae; tibiae with longitudinal rows of spines in apical third only, spines thin; middle tibia without apical cleaning brush; tibial spurs (Fig. 7B:ts) spatulate. Tarsomeres 1–4 each with many stiff setae laterally, ventrally, and apically; tarsomere 5 (Fig. 7C) elongate, longer than tarsomeres 2–4, ventrally with row of setae on lateral margins; tarsal claws average size for broscines of this length, curved; unguitactor plate broad, flat, rounded at apex. Male fore and middle tarsomeres without adhesive vestiture ventrally.

Abdominal Sterna.—As in most Carabidae, but ambulatory setae absent from sterna IV, V, and VI; sternum VII with single pair of setae preapically; sterna III and IV laterally with surfaces depressed, depressions occupied by basal parts of legs; sterna V–VII each near anterior margin with deep transverse groove. Sternum VII of male (Fig. 9B) very broadly rounded apically, female (Fig. 9C) much more narrowly and abruptly rounded.

Male Genitalia.—Median lobe (Fig. 10A, B:ml) as in most Broscina: basal opening wide, extended onto dorsal surface, margins nearly truncate in lateral aspect; dorsal membrane extensive; apical portion in ventral aspect tapered to a narrow point (Fig. 10C). Internal sac (Fig. 10A, B, F–H) with sclerites x and y, and apical plate (a) (Ball, 1956:48, fig. 3) with large and complex microtrichial field (Fig. 10F–H); gonopore (go) positioned as in Fig. 10H in complex folds at apex of sac; sclerite x basally not constricted, and with pair of flanges extended apically; apically, in dorsal aspect, tapered evenly to blunt point, neither constricted abruptly, nor terminated in subuliform projection (Fig. 10F, G:x, f). Parameres (Fig. 10D, E) long, left styliform (Fig. 10A, B, D:lp), basally broader than right, each tapered apically, and each setose in apical third.

Spermatophore.—Elongate and irregular (Fig. 11B, C:spa), shaped as in Figure 11B and apparently attached near spermathecal opening.

Ovipositor.—Stylomere 2 shorter than stylomere 1 (Fig. 7D, 11A:s-1, s-2). Stylomere 1 with several setae apically, on medial side. Stylomere 2 (Fig. 7E, F) with apex tapered to bluntly rounded tip; margins without ensiform setae; ventral surface (Fig. 7F, G) with sensory pit long, narrow, with two short nematiform setae (ns) and several pit pegs (spp). Ramus lacking mesad stylomere 1.

Internal Reproductive Organs, Female.—Reproductive tract (Fig. 11A, C) with bursa copulatrix (bc) elongate, with long spermathecal gland (sg); spermatheca (sp) moderately long, at base with helminthoid bursal sclerite (hsc). Spermatheca and spermathecal gland entering bursa separately.

Note on Presumed Spermatophore

The structure illustrated in Fig. 11B was removed from the bursa copulatrix of a female. We assume it to be a spermatophore. Little is known about spermatophore

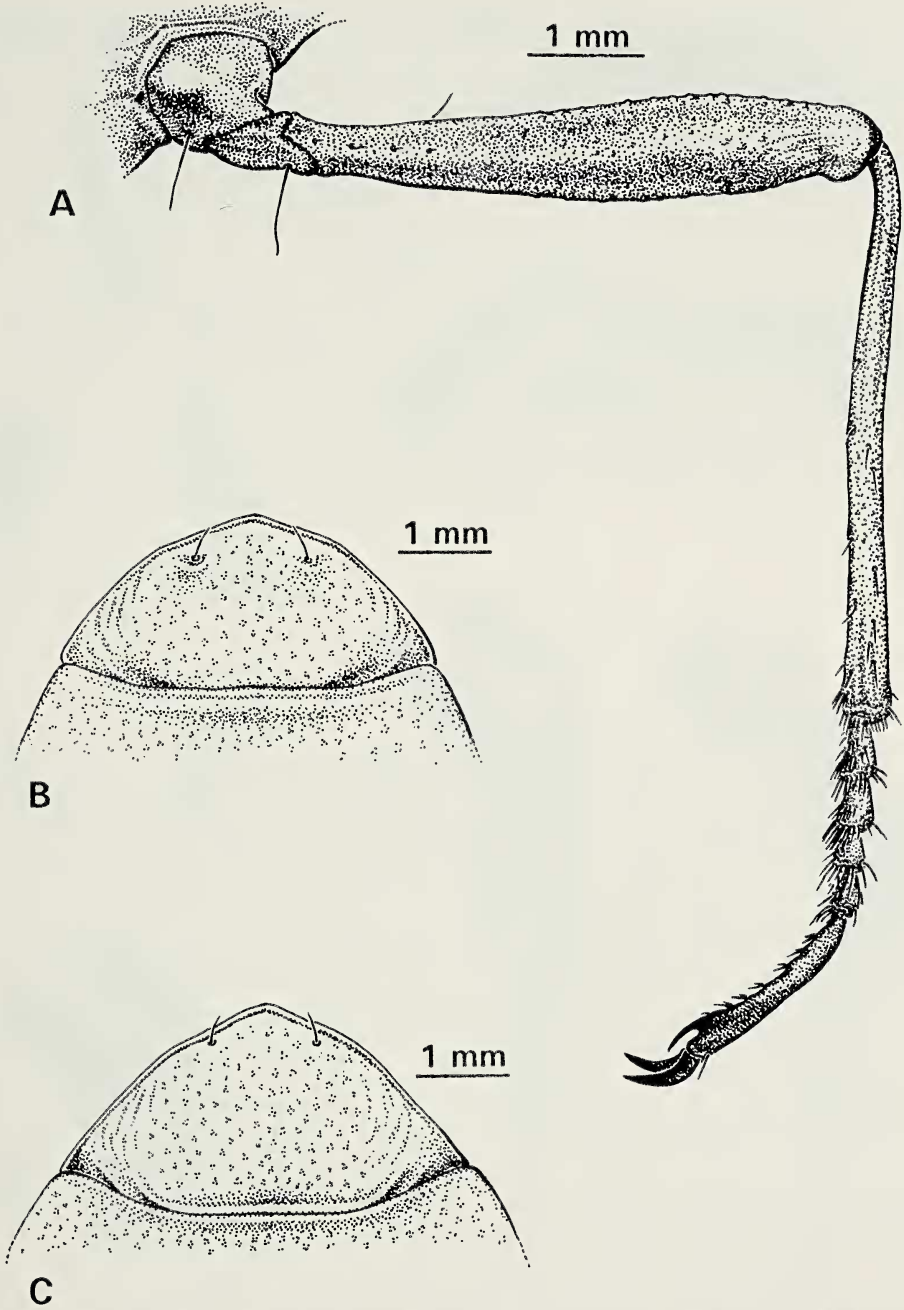


Fig. 9.—Line drawings of leg and abdominal sternum VII of *Rawlinsius papillatus*, n. gen., n. sp. A, left middle leg, anterior aspect. B, abdominal sternum VII of male, ventral aspect. C, abdominal sternum VII, female, ventral aspect.

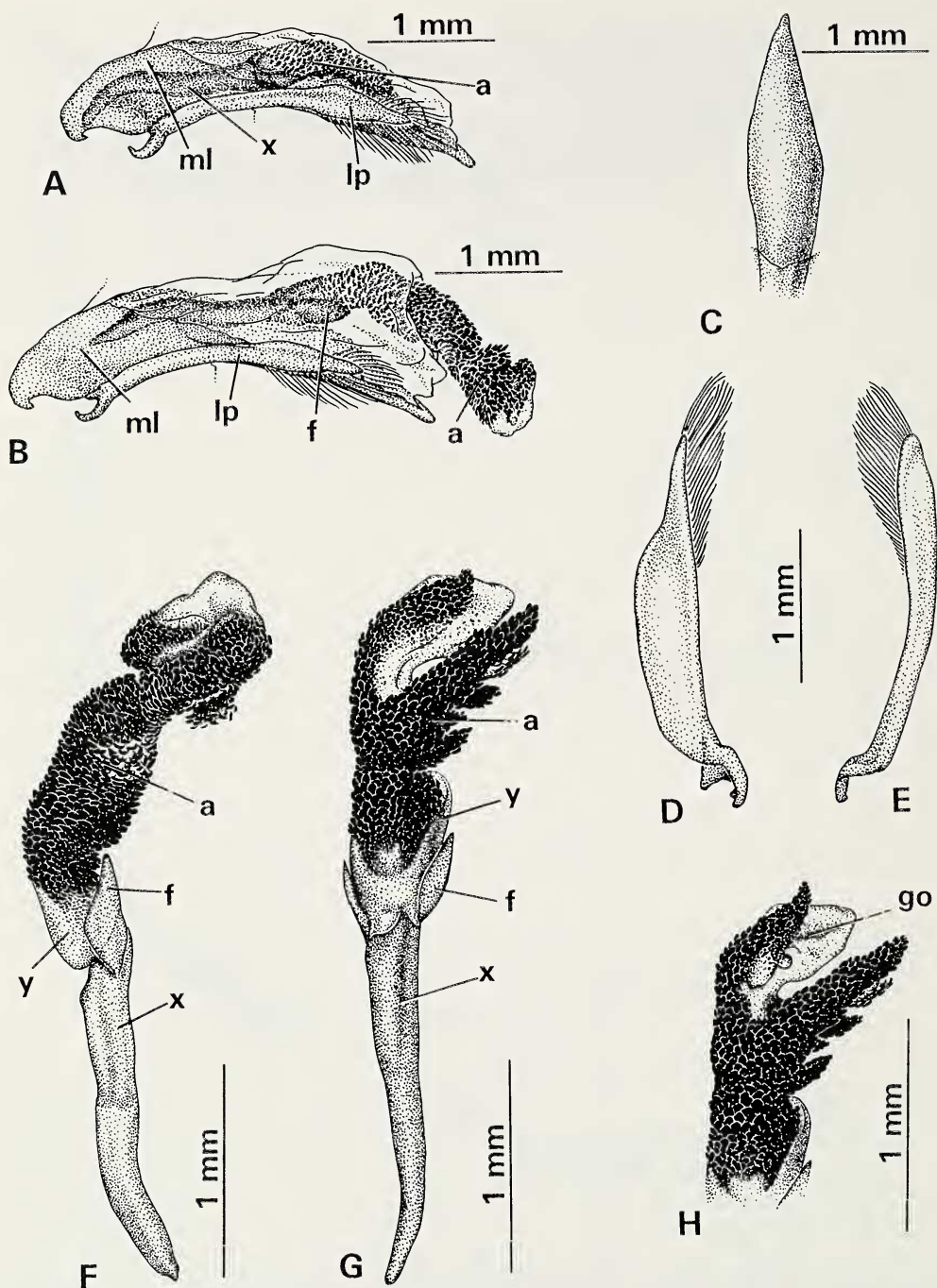


Fig. 10.—Line drawings of male genitalia of *Rawlinsius papillatus*, n. gen., n. sp. A, median lobe and armature of internal sac completely inverted, left lateral aspect. B, same, but internal sac partially everted. C, median lobe, apical portion, ventral aspect. D, E, left and right parameres, respectively, ventral aspect. F, G, H, armature of internal sac, everted: F, left lateral aspect; G, dorsal aspect; H, apical portion, left lateral aspect. Abbreviations: a, apical plate, showing microtrichial field; f, lateral flange of sclerite; x, gonopore; lp, left paramere; ml, median lobe; x, y, sclerites of internal sac.

phores in Carabidae. Crowson (1981:401) asserted that, in Coleoptera, the most common mode of sperm transmission is "in the form of packets or spermatophores." Jeannel (1928:356–357, footnote 1) discussed the evolutionary significance of spermatophores generally, and illustrated one (fig. 1725) for a species of trechine carabid. He stated that finding a spermatophore was a rare event, and that he had seen only one in the numerous dissections of carabid males that he had made. We examined the bursae of two other female *Rawlinsius*. They each contained a transparent bag, probably the remnants of spent spermatophores.

Geographical Distribution

Known only from the type locality (Fig. 12), in Guerrero, Mexico, the species is expected to occur in suitable habitat throughout at least the south face of the Sierra de Atoyac de Alvarez and probably throughout the Sierra Madre del Sur in Guerrero and into Oaxaca. It or a related species might also be in Guatemala. The species *Hyperthaema sororita* Schaus (Lepidoptera: Arctiidae), thought to be precinctive to Guatemala (J. E. Rawlins, personal communication), was taken at the broscine site during both trips (1981, 1986).

Phylogenetic Relationships

See topic under generic treatment.

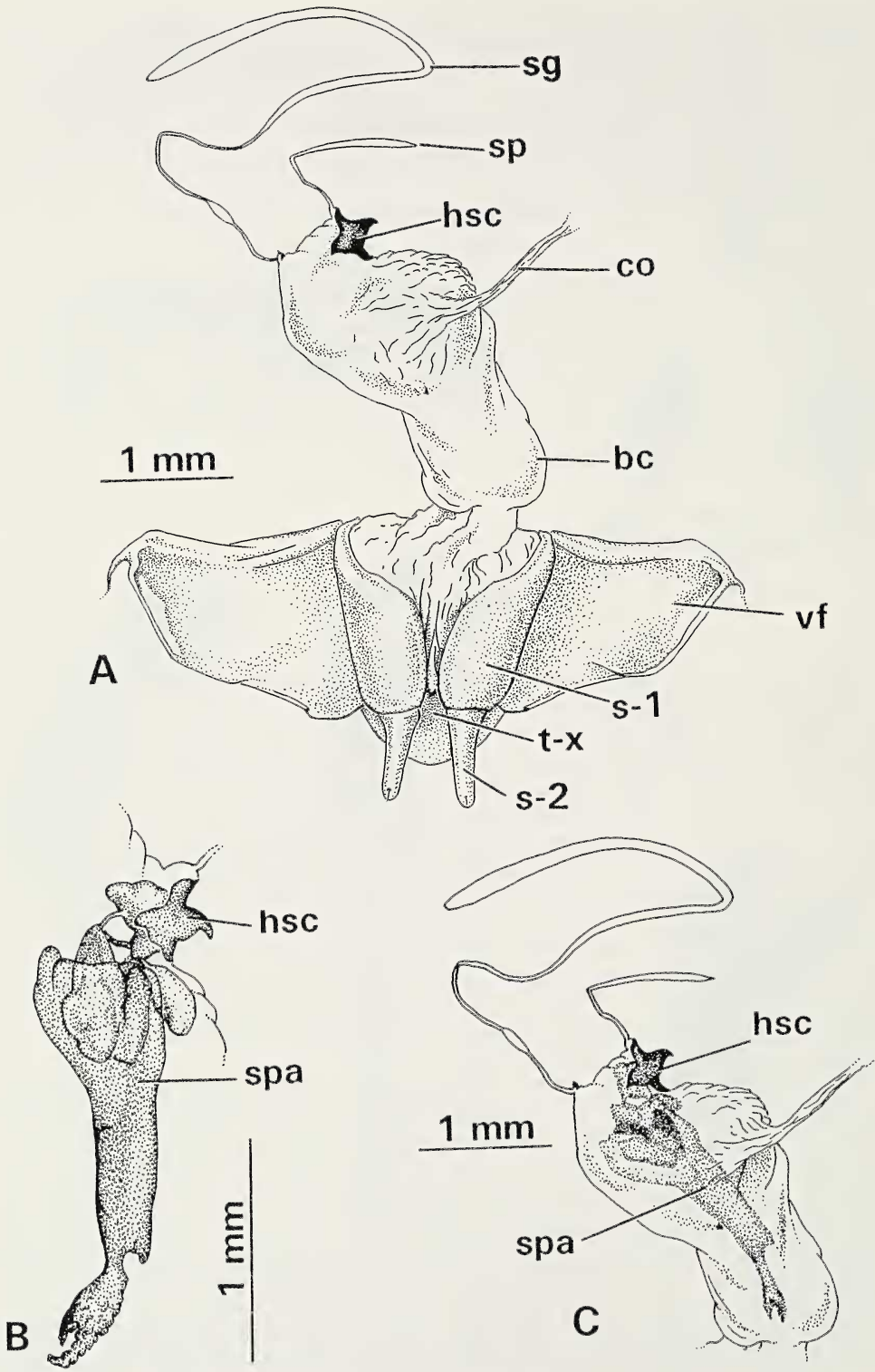
NATURAL HISTORY

Habitat

The beetles were taken in the overflow of a small stream that flowed down a steep gradient off the mountain until it intersected a road cut which formed a cliff about 3 m high. At the road cut, the main channel formed a small waterfall jetting on to the road, and the water then flowed across the road and down the cliff on the downhill side. The steep gradient did not allow access to the stream except where it flowed over the 3-m cliff on the uphill side of the road. In this area, the edges of the stream formed thin sheets of running water at the crest of the cliff and along the vertical rock face to the sides of the waterfall. Three adults and one larva were found in this area, near the top of the cliff. A small finger of water, segregated from the main stream above the cliff, spread into a thin sheet of fast-running water. This flowed down the vertical rock face about 4 m to the left (viewed facing uphill) of the main channel, forming a thin vertical sheet of fast-running water about a meter wide and 3 m high (Fig. 3C). The lush growth of mosses and algae in this flow suggest it is relatively permanent. Ten adults and one larva were found in this tiny area.

The nature of the terrain and the equipment at hand did not permit sampling above or below the road cut. It was impossible to determine whether beetles occurred only on the vertical wet faces or might also be present in shallow water along the steep gradient (where much water flowed in thin sheets across bare rock) or the occasional flat benches visible above. The stream above flowed in thin sheets down several vertical faces and steep slopes, any of which might have been suitable habitat. No beetles were found in the deeper water of the main channel, but this too was accessible only at the crest of the roadside cliff. It was impossible to check the main channel in flatter places above.

Three other streams along the same road (two near the same altitude, one a few hundred meters lower) were searched unsuccessfully for these beetles, both



during the day and at night. Two of the streams were quite different in character, flowing under dense vegetation or with more typical boulder outcrops and sandy or gravelly bottoms and banks. The third stream was similar to the broscine stream in some respects as it flowed over sloping bare rock in places, but it lacked the vertical faces and the thin sheets of flowing water. The apparent absence of *R. papillatus* in these streams suggests that the beetles are very particular about microhabitat.

Voucher specimens were taken of plants growing in the small patch of water where most of the beetles were collected. The dominant plants were several mosses (including *Anomobryum plicatum* Card. [Bryaceae] and *Breutelia* sp. [Bartramiaceae]), a species of *Selaginella* (Selaginellaceae), *Pilea* sp. (Urticaceae), *Campylongus oblongus* (Dicranaceae), and an undetermined sedge (Cyperaceae) (voucher specimens in Carnegie Museum Herbarium, *Rawlins & Davidson 285 to 290*). These are all plants characteristic of permanently wet microsites. A hydrophilid beetle (*Cymbiodyta brevipalpus* Smetana) was also common in the same microhabitat.

The general surrounding habitat was Lower Cloud Forest typical of the Sierra de Atoyac de Alvarez at middle altitudes. The area has been described in some detail by Vargas-Fernandez et al. (1992).

Behavior

These beetles forage, feed, and mate at night in shallow sheets of running water on sheer rock faces. Adults, active in the water after dark, were not found in the daytime, probably having retreated into deep crevices in the surrounding rock. It is unlikely that they spend the day in the water or even very close to the water. Davidson and Rawlins studied several individuals (Fig. 3A, B) at night in their natural habitat and in captivity during the day.

In the first observations (just after dark) of these beetles in 1986, seven or eight individuals were fairly evenly distributed over the main part of the small area of habitat. Exposed to the lights, many of them began to move toward the edges and into the darkness and vegetation. Removal of the lights for a time permitted them to settle, and keeping them in the dimmer edge of the beam allowed most of the observations discussed below without apparent disturbance.

The beetles moved in two very different manners. Most of them remained under water most of the time. They bent the legs such that the venter of the body was pressed flat against the rock, and the water running over their backs helped keep them appressed against the substrate. In this position, they moved very quickly under the water like tiny submarines. They moved upstream, downstream, and cross-current with equal ease, as far as the observers could tell. Several individuals poked their heads into clumps of moss or algae as if searching for food, and on at least two occasions beetles seemed to be capturing something. The observers

←

Fig. 11.—Line drawings, ventral aspect, of ovipositor and internal reproductive organs of female, and male spermatophore, of *Rawlinsius papillatus*, n. gen., n. sp. A, bursa copulatrix and associated structures, ventral aspect, $\times 25$. B, spermatophore of male, ventral aspect. C, bursa copulatrix with spermatophore, ventral aspect. Abbreviations: sg, spermathecal gland of bursa copulatrix; bc, bursa copulatrix; co, common oviduct; s-1, s-2, ovipositor, stylomeres 1 and 2, respectively; hsc, helminthoid sclerite at base of spermatheca; sp, spermatheca; spa, spermatophore; t-x, tergum X; vf, valvifer.

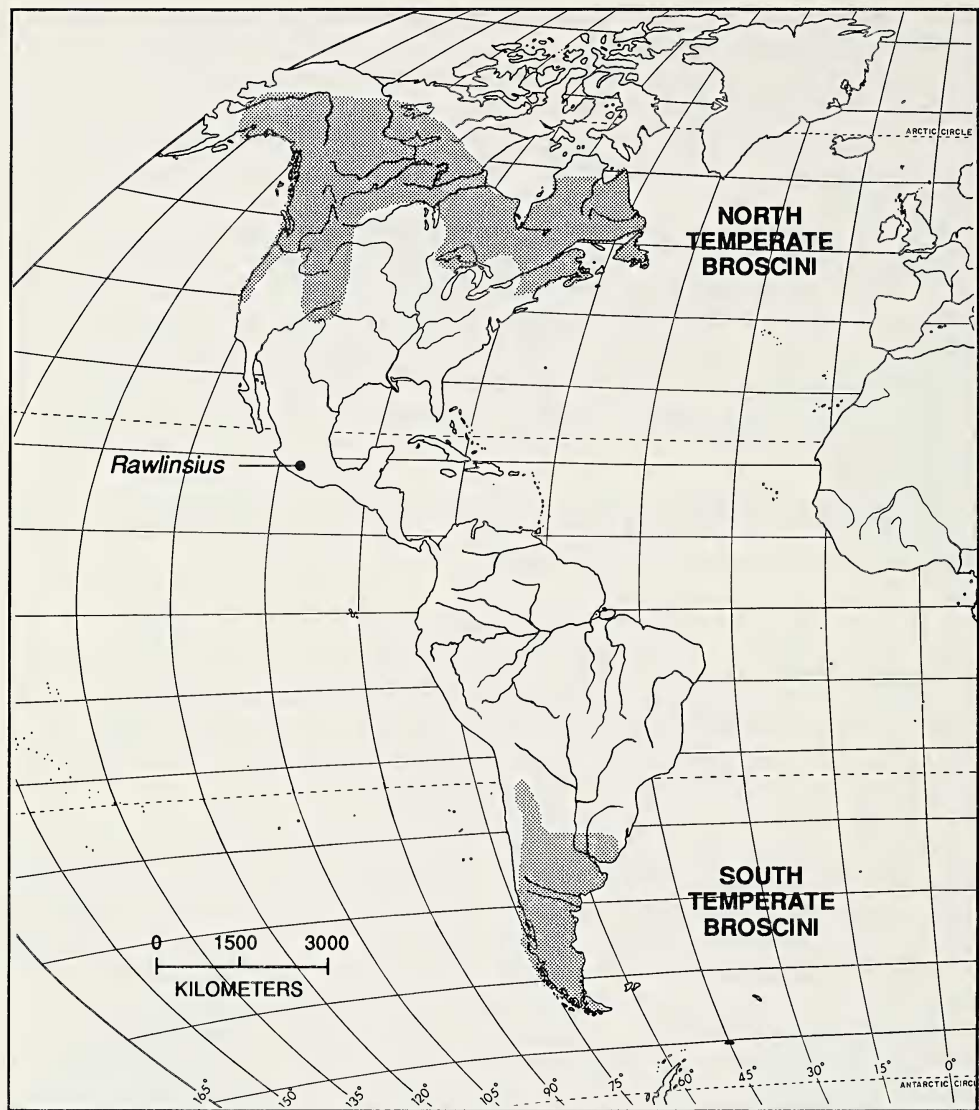


Fig. 12.—Generalized geographical range of the tribe Broscini in the Western Hemisphere.

could not see what the beetles were capturing, but it was most probably tiny Diptera larvae, nematodes, or some other soft invertebrates.

Three individuals used a second manner of locomotion, wading through the water with their bodies above the current, much like a wading bird. The water was so shallow it came only to the middle of the tibiae when the beetles stood up. These individuals stepped quickly through the water, and two individuals thrust their heads under water into clumps of vegetation, presumably searching for food.

Two larvae also were observed briefly. Their movement was quite different from that of the adults. They did not submerge themselves but ran quickly through

the water and several times completely out of the water over the surface of the mosses. Their movement was very frenetic and erratic, faster than the adults, with frequent shifts of direction and frequent plunging of the mandibles and head into vegetation, both above and below water. Foraging on above-water mosses, most of a larva would sometimes disappear into the vegetation. Adult movement, although fast, was much more deliberate, steady, and relatively one-directional.

Two pairs of adults were observed in copulation in the water. One pair was not tightly coupled and broke apart within a few seconds of exposure to the headlamps. The second pair remained coupled, the female under water against the rock, the male on top. Most of the male was above the water surface, as the water was too shallow for both individuals to be submerged.

A few individuals were placed alive in small plastic containers with moss, sand, and rock, on the surfaces of which the beetles moved freely. On several occasions, they lifted the elytra, flexed the flight wings, and tried to fly, colliding with the lid of the container. Adults are clearly capable of flight and must at times disperse up and down the stream or search for other suitable streams. They must do this, however, only at certain times or under certain conditions. An ultraviolet light trap, operated for two nights within 2 m of the habitat, did not attract any of these beetles. This suggests they may not come to ultraviolet light or may do so only when they are prone to flight. It is not known whether flight is frequent and routine, seasonal, weather dependent, or habitat dependent (e.g., lowering stream water level or shifting of stream course).

EVOLUTIONARY ASPECTS

Adaptations

The loss of virtually all normal dorsal setae, presence of which is characteristic of Carabidae, is undoubtedly an adaptation to the unique habitat of *R. papillatus*. Many carabids (e.g., Oodini, Chlaeniini, various Palaearctic species of *Carabus* Linnaeus [Thiele, 1977:218–220]) are active under standing water of swamps, bogs, and wetlands. Several species specialize in splash zones of rapids and waterfalls (e.g., some *Platynus* Bonelli, *Bembidion rufotinctum* Chaudoir, *Pterostichus johnsoni* Ulke). All of these have setation normal for their tribes. Adults of the western North American nebriine, *Nebria ingens* Horn, walk on the substrate underwater in fast-flowing streams and exhibit adaptations in the form of tarsal shape and reduced ventral vestiture (Kavanaugh, 1978). Like *Nebria ingens*, *Rawlinsius papillatus* actively forage under fast-moving water but seem more highly specialized for that role. The only other broscine known to us that seems to be associated with aquatic habitats is *Axonya championi* Andrewes, an Indian species. In his original description, Andrewes (1923:681) refers to a letter from Champion as follows: "Common on river banks in wet places. Runs freely on the water." We cannot tell from this brief remark exactly how aquatic *Axonya* might be.

The tarsal claws (Fig. 7C) seemed to be disproportionately large, much like the tarsal claws characteristic of adult elmids beetles. Measurement of the claws of other broscines proved that *R. papillatus* claws are of average size for a broscine of that length, but the very slender and much elongated legs give the impression of larger claws. Most broscines have robust, stout, relatively short legs. The long, thin legs (Fig. 9A) of *R. papillatus* present less surface resistance to running water, allow the beetle to press its ventral surface against the rock for movement under

water, and allow it to stand upright as if on stilts to wade with its body above the water. Maintaining the claw size when the legs (evolutionarily) have been thinned and elongated leaves a relatively large claw for clinging to rock, and probably the numerous stiff bristles on the ventral side of tarsomeres 1–4 help with movement and attachment. The claws are curved, which no doubt helps the beetle cling to the rock.

The surface of the elytra with extraordinary microsculpture and nipplelike bumps (each with a tiny seta; Fig. 4A–E) is unique in Carabidae so far as we know. The cuticle wets easily and retains a film of water that engulfs the body completely. Most broscine males have some protarsal adhesive vestiture (and some species have some mesotarsal vestiture as well), although markedly reduced in some taxa (e.g., *Nothocascellius hyadesii* [Fairmaire], with only a tiny patch each on protarsomeres 1 and 2 [Roig Juñent, 1995]). Male adhesive vestiture of the protarsi is lost entirely in *R. papillatus*, possibly for the same reasons the dorsal setae are lost, or possibly because the protarsal pads do not function well in gripping the female while mating under water.

The structure of the mouthparts does not indicate external digestion. The mandibles have a short ventral groove (Fig. 5E:vg) and are equipped with short and relatively few microtrichia. The maxillary laciniae (Fig. 6C:la) have long, stiff setae and lack a dense brush of setae, and the epipharynx (Fig. 6B) is reduced. If the beetles feed primarily or at least frequently under running water, external digestion is probably impossible, and the mouthparts certainly suggest that digestion is internal.

The macropterous condition, including body proportions indicative of flying ability (relatively small fore body and hind body with long elytra and large metathorax), is a retained plesiomorphy, with flight being essential for beetles that live in intrinsically unstable riparian habitats.

The adaptive significance of some structures of the female genitalia is not clear, but they will be important in understanding broscine relationships. We therefore discuss briefly three of these structures. In the higher Carabidae (e.g., tribes Pterostichini, Platynini, Oodini, Chlaeniini, Lebiini), the spermatheca and spermathecal gland are joined before their common entry into the bursa. In broscine genera studied (see Deuve, 1993:153–156), including *Rawlinsius*, the spermathecal gland (when present) and the spermatheca enter the bursa separately. This may be the ground plan of the Broscini. Another structure, the ramus (see Bills, 1976, for definition of this term), is plesiomorphically present mesad stylomere 1 (Liebherr and Will, in press). Liebherr and Will found rami in species of *Broscus* and *Zacotus*, and Deuve (1993:154, fig. 235, 237) shows rami in *Broscus* and *Metaglymma* Bates. Deuve (1993:154–155, fig. 238, 239, 241, 242) shows no rami in *Percosoma* Schaum, *Cascellius*, *Broscosoma* Rosenhauer, or *Miscodera*. No doubt substantial dissection is required to determine how this influences broscine relationships. It is important to note that *Rawlinsius* lacks such structures, and that this is synapomorphous within the tribe.

Phylogenetic Interpretation of Adaptive Features

Absence of setae, presence of elytral papillae, and long, slender legs are interpreted as apomorphic features, developed as adaptations for life in close association with running water. Perhaps ancestral broscines were associated with riparian situations, as is *Axonya championi* Andrewes (Andrewes, 1923), and perhaps

Rawlinsius is a survivor of an ancestral riparian lineage. This would fit with the Darlington–Erwin concept of taxon pulses, in which new carabid lineages (specifically) evolved initially in “equatorial wetlands” (Erwin, 1985:462; see also p. 445, fig. 2) and sequentially came to occupy other habitats and other parts of the world, eventually with the primitive riparian lineages becoming extinct in the face of competition from later-evolving and more successful groups. *Rawlinsius* managed to survive in the ancestral zone by evolving to occupy a very special and restricted part of it; it has, so to speak, retained its hold on the central zone of carabid evolution by becoming slightly peripheral. Maintenance of the flight apparatus is very interesting. Although certainly adaptive at an earlier point in the history of the evolution of Carabidae or Coleoptera, it is in Broscini a plesiomorphic feature. Its retention in *Rawlinsius papillatus* was a functional necessity and reflects the precarious nature of the habitat.

Chorological Features

Itself a geographical relict, in the sense of its wide isolation from other broscines (see Fig. 12), and a phylogenetic relict, in the sense that it may be the lone survivor of a primitive broscine stock (see Simpson, 1944:144–145 and Brooks and McLennan, 1991:128 and 256–259, for discussions of the term “relict”), the genus *Rawlinsius* is known only from a region (the Sierra de Atoyac de Alvarez) that is rich in precinctive taxa (see, for example, Vargas-Fernandez et al., 1992; Llorente-Bousquets and Luis-Martinez, 1993). More generally, the mountains of southern Mexico, particularly the humid temperate forests (within which zone *Rawlinsius* occurs) are noted for an appreciable amount of precinctive taxa. Among such groups are various carabid lineages that are also geographical and/or phylogenetic relicts (Table 1). Within this geographical group, however, *Rawlinsius* is unique, being the only precinctive representative of its entire tribe to occur within this region.

These relict taxa are either monobasic or polybasic, ranging in rank from species to genus. The polybasic groups evidently have differentiated within the mountains of southern Mexico, whereas the monobasic groups either have not differentiated, or are sole survivors of the taxon to which each belongs.

The species *Nomius pygmaeus* (Dejean), with the most extensive part of its range occurring to the north, evidently has not differentiated. It is a relict at the population, rather than taxon, level. The monobasic *Galerita sulcipennis* group, subgenus *Tachalus* Ball and Nègre, and genus *Rawlinsius* are relicts at the taxonomic level, and may be survivors of lineages that were once more speciose. In any event, it seems reasonable to infer that *N. pygmaeus* is a relatively recent (Pleistocene age) arrival in southern Mexico, whereas the latter three groups arrived in the area at a substantially earlier time (Paleocene to Miocene).

As emphasized by Liebherr (1994:842), carabid taxa occupying the humid temperate forest zone in southern Mexico have either southern or northern roots. Of the taxa in Table 1, six are northern (including *Rawlinsius*) and five are southern in affinity. They represent three major distribution patterns recognized by Halffter (1987; see also Kohlmann and Halffter, 1990): the Nearctic pattern (for northern elements of more recent arrival), the Paleo-American pattern (for older northern elements), and the Meso-American Montane pattern (for southern elements reported here). Of the taxa listed in Table 1, then, *Nomius pygmaeus* represents the Nearctic pattern; *Tachalus*, *Rawlinsius*, and the *Hypherpes*-like taxa, the Paleo-

Table 1.—*Geographical relict taxa of Carabidae in southern Mexico.*

| Taxon | Rank | Affinity | | Reference |
|--|-----------------------------------|----------|-------|---------------------------------|
| | | North | South | |
| <i>Nomius pygmaeus</i> Dejean | Species | X | | Ball, 1977:394-395 ¹ |
| <i>Eucheila cordova</i> Ball and Shpeley | Species | | X | Ball and Shpeley, 1983:802 |
| <i>Galerita sulcipennis</i> Reichardt | Species group (monobasic) | | X | Ball, 1985:317 |
| <i>Tachalus</i> Ball and Nègre | Subgenus (monobasic) ² | X | | Ball and Nègre, 1972:423 |
| Hypherpes-like taxa ³ | Three subgenera (polybasic) | X | | Ball and Roughley, 1982 |
| <i>Eripus</i> Dejean | Subgenus (polybasic) | | X | Straneo and Ball, 1989:153 |
| <i>Cyrtolaus</i> Bates | Genus (polybasic) | | X | Liebherr, 1986:95 |
| <i>Dyschromus</i> Chaudoir | Genus (polybasic) | | X | Unpublished |
| <i>Rawlinsius</i> Davidson and Ball | Genus (monobasic) | X | | This paper |

¹ Bousquet and Laroche (1993:158) provide a synopsis by states and provinces of the U. S. and Canadian range of this species; transcontinental in the northern boreal forest, southward to Georgia in the east, and southern Arizona and California in the west.

² For a different interpretation of the relationships of this taxon (as *Calathus ovipennis* Putzeys), see Liebherr (1994:848, fig. 10).

³ The subgenera included are: *Percolaus* Bates (Ball and Roughley, 1982:327), *Mayaferonia* Ball and Roughley (1992:336), and *Allotriopus* Bates (Ball and Roughley, 1982:349). They belong to the northern genus *Pterostichus* Bonelli. Adults of the three subgenera are similar to one another in body form, and to the Nearctic subgenus *Hypherpes* Chaudoir. Relationships of these taxa to one another have not been established.

American pattern; and *Eucheila cordova* Ball and Shpeley, *Galerita sulcipennis* species group, *Eripus* Dejean, *Cyrtolaus* Bates, and *Dyschromus* Chaudoir, the Meso-American Montane pattern. The details of the Meso-American Montane pattern are of no further interest in the present context.

The relict status of the northern-based taxa suggests marked changes of some type that led to their isolation in the Mexican highlands, possibly drying of the intervening areas, with associated changes in vegetation. The fact that at least two different ages of dispersal are indicated suggests that either the climatic changes were cyclic in nature, or that the later-arriving *N. pygmaeus* had different adaptations from the earlier arrivals, and was thus able to spread southward. Ball and Nègre (1972:528) and more recent authors (e.g., Jameson 1990:412) hypothesized cyclic climatic changes within northern Mexico, resulting in conditions favorable for dispersal alternating with unfavorable conditions that resulted in more or less extensive range disruption with consequent differentiation of isolated populations that managed to survive in favorable areas or refugia.

We believe, then, that the ancestral *Broschina* were widespread in North America, and were possibly riparian in habitat preference. Unfavorable climatic conditions led to extinction of the *Broschina* over large parts of North America, with a single lineage persisting in southern Mexico. To the north, in western North America, one or more lineages survived and differentiated, but the descendants did not evolve the adaptations required to recover the whole of the ancestral range. Similarly, the Mexican lineage became highly specialized to live in association with fast-flowing water, and is thus unable to re-occupy the ancestral range in lowlands.

CONCLUDING REMARKS

The discovery of *Rawlinsius papillatus* was an exciting event in the development of knowledge of the Middle American carabid fauna. Additional populations of this species are not likely to be encountered casually and therefore the species may have a much wider range than known currently. Specimens probably will be found only at night, in very patchy microhabitats, mostly difficult of access. They are likely to be found only by the most energetic and persistent collectors, and then only with a good deal of luck. We hope that the discovery of this species will encourage adventurous collectors to search vigorously for further localities or additional species of *Rawlinsius* throughout southern Mexico, Central America, and perhaps even the northern mountains of South America. A taxon with such secretive and elusive members could turn up in any of the mountain ranges that add so much wonder and beauty to the tropics of the New World.

This remarkable relictual species forces attention on the area in which it is known to live—the Sierra de Atoyac de Alvarez. This mountain range, as well as the other parts of the Sierra Madre del Sur, gives evidence of a substantial amount of precinction, especially at higher altitudes. With extensive tracts of forest still intact, this mountain range would seem to be prime ground for establishment of an ecological reserve, as well as the focal point for extensive exploration of its fauna and flora. Undertaking such activities is a challenge for the government of Mexico, and for the Mexican biologists who are interested in biodiversity, the country's "rich biological patrimony" (Toledo and Ordoñez, 1993:775).

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